COYOTE POPULATION PROCESSES REVISITED

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Abstract: It appears that coyote (*Canis latrans*) abundance is determined primarily by availability of food (prey) as mediated through social dominance hierarchies and a territorial land tenure system. This is reflected in rates of reproduction, dispersal, and mortality, with survival of juveniles a major factor. Suggestions for a new generation of simulation models to explore coyote population functions are included.

Population manipulation is a prominent component of many coyote management programs. Understanding the factors affecting animal abundance and the mechanisms of population regulation can assist in recognizing the merits and liabilities associated with such management approaches. In turn, this should help identify more flexible management scenarios and result in management programs that are more selective, effective and efficient.

Gier (1968) and Knowlton (1972) provided some initial information on coyote population parameters. Additional information from a variety of authors lead Knowlton and Stoddart (1983) to hypothesize that coyote abundance was governed by interactions between available food (prey) and coyote behavioral characteristics, namely social dominance and territoriality, with the impact expressed through the processes of reproduction, mortality, ingress and egress. Similar conclusions were reached by Packard and Mech (1983) to explain population regulation in grey wolves (*C. lupus*). Herein we review these ideas in light of information acquired in recent years.

Evidence concerning food abundance

Knowlton and Stoddart (1983) used 3 lines of evidence to support the contention that food abundance was a major determinant of coyote abundance, namely: (1) state by state averages of the indices of coyote abundance calculated from the Westwide Survey of Predator Abundance (Linhart and Knowlton 1975, Roughton and Sweeny 1982); (2) a meager data set concerning coyote and rodent abundance on sites scattered throughout Texas; and (3) a 15-year time series of coyote and jackrabbit (*Lepus californicus*) density estimates in Curlew Valley, Utah.

Since the previous paper, the data set for the first has not changed and prior interpretations remain largely intact, i.e., mean coyote abundance varies among the western states and appears to reflect primary productivity. Higher densities occur in the Great Plains, a relative scarcity typifies the intermountain region, and moderate abundances are found among the states of the Pacific coast. In addition, an increasing kline in density from northern to southern states seems evident. This appears consistent with observations by Weaver (1979) and Todd and Keith (1976) suggesting food supplies in winter may be particularly important in areas where conditions are more harsh. Gese (1995) identified available food resources in winter to be particularly important in regulating size of coyote packs in Yellowstone National Park.

The second data set, concerning the relative abundance of coyotes and rodents on sites throughout Texas has not been elaborated and is unconvincing on its own. However, the results are consistent with other sources of information.

Since the earlier paper, annual and semi-annual density estimates for coyotes and jackrabbits in Curlew Valley, Utah, were extended to 28 years. That data set includes information indicating the irruption in jackrabbit numbers that peaked in 1980 subsided to very low numbers by the mid-1980s and was followed by another irruption in the early 1990s.

Coyote numbers, however, did not follow the anticipated patterns. When jackrabbit numbers declined in the mid-1980s, coyote numbers remained high. Faced with explaining deviance from the expected, 2 hypotheses were identified. The first suggesting this resulted from a marked increase in

the abundance of deer and antelope in Curlew Valley, providing an alternate winter food resource. The other hypothesis involved lower mortality rates associated with reduced human exploitation resulting from lower fur prices and a reduction in the intensity of exploitation to protect domestic stock. Although our current preference resides with the first alternative and is consistent with the food abundance hypothesis, no additional data have been assembled to clarify the issues. On the other hand, Hamlin et al. (1989) reported that during a population decline of mule deer (*Odocoileus hemionus*) in north-central Montana, coyotes remained abundant. They hypothesized that coyote survival may have increased as a result of increased abundance of microtine rodents as an alternative food source. This was unlikely in Curlew Valley because microtines are not common (Hoffman 1979).

Other studies have added to our understandings. A companion study to the Curlew Valley research involved monitoring rodent, lagomorph, and coyote populations over a 12-year period on the Idaho National Engineering Laboratory (INEL), a site some 100 miles north of Curlew Valley and largely immune from public access (Stoddart 1987). Data from this location are similar to those from Curlew Valley, with jackrabbit populations irrupting from extremely low numbers in the late 1970s to over 280 per mi^2 in 1981, and then returning to very low levels by the mid 1980s. Coincident with the increase in hares, coyote abundance increased 5-fold, followed by a gradual decline after hares became scarce. This reinforces previous interpretations about the potential role of prey abundance in determining coyote abundance.

One notable aspect of the INEL data is the relatively slow response in coyote abundance to the abrupt decline in a major food resource. Two years after the jackrabbit population returned to very low levels, the spring coyote density index was still 3 times pre-irruption levels. Todd et al. (1981) and Todd and Keith (1983) found that winter coyote abundance was directly related to snowshoe hare abundance. In their study, all demographic parameters of coyotes measured declined as snowshoe hares became scarce, leading them to believe that low availability of alternate prey in the boreal forest intimately linked the coyote population to fluctuations in snowshoe hare abundance.

Based on an 11-year study in southern Texas, Windberg (1995) provided data indicating coyote

population growth was correlated positively with winter prey abundance and correlated negatively with initial coyote abundance. Since both prey and coyotes were extremely abundant in the area (spring coyote populations estimated at 4-7 per mi^2), the coyote population may have been approaching the upper limits for density and other constraints may have also been operating. This study is particularly notable in that it documents a negative relationship between coyote abundance and population growth.

Although convictions that a relationship between coyote abundance and prey abundance have been reinforced in recent years, more definitive understandings of that relationship have not emerged. Improved quantitative assessments of the abundance and availability of prey in relation to coyote density, along with the adoption of standardized methodology among studies are needed to provide more enlightenment. Long-term monitoring of predator and prey populations will be essential to clarify the impacts and mechanism(s) linking predator and prey populations.

The social dynamic

Knowledge about coyote sociodemography that was budding at the time of Knowlton and Stoddart's 1983 paper has blossomed. The territorialism initially espoused by Camenzind (1978) and Bowen (1978, 1982), in which packs of coyotes defend areas against intrusions of others has been enhanced by the studies of Andelt (1982, 1985), Crabtree (1988), and Windberg and Knowlton (1988).

Our current understanding indicates that habitat suitable for coyotes is partitioned among territorial social groups of 2-7, frequently related, adult coyotes. These territories are typically contiguous and apparently defended against intrusions from coyotes not belonging to the territorial social group (Gese 1995). Non-territorial individuals are a cadre of transient, typically solitary, individuals living among the interstices of the territories. Transients sometimes trespass upon the territories, and occasionally form temporary liaisons with various territorial groups. These coyotes appear to be "biding their time", trying to fit into the more stable portion of the population.

Data from Andelt (1985), Crabtree (1988), Windberg and Knowlton (1988) and Gese (1995) show that being territorial and socially dominant are

common prerequisites for the successful nurture of young. Although subordinate and non-territorial individuals may become reproductively active, their likelihood of reproductive success is very low. There is also a suggestion that territories are inherited from one generation to the next, with territorial boundaries remaining intact well beyond the lives of individual inhabitants.

Territorial patterns among coyotes in high mountain areas deserve some mention because conventional wisdom frequently suggests coyotes living at high elevations in summer accompany migrating large ungulates to wintering areas at lower elevations. If this occurred, coyotes would seemingly be "off territory" during courtship, breeding, and early post-whelping periods; times when territoriality should convey its greatest advantages. Gantz (1990) specifically studied this aspect and found adult coyotes in the mountains of northern Utah used the same areas in summer and winter, even at altitudes exceeding 7,500 feet. Shivik (1995), working in the Sierra Nevada, similarly reported coyotes maintaining territories at high elevations in winter. This is consistent with Weaver's (1979) interpretations that coyotes live in summer where they can survive in winter.

Demography of populations immune from human exploitation

Another significant aspect of coyote population biology is currently emerging, i.e., characteristics of unexploited populations. In retrospect, initial glimpses can be recognized in a Knowlton (1972) as well as unpublished data on coyote population structures in southern New Mexico and Arizona collected by Sam Linhart in the early 1970s. However, the significance of these data were not recognized at the time.

More recent studies (Crabtree 1988, Windberg 1995, Windberg et al. [In draft], Gese et al. 1989) suggest unexploited populations may be functionally and structurally different from information published previously. Although verification is pending, the emerging pattern suggests that in saturated populations, territorial coyotes have relatively long tenures with very low reproductive rates (Gese 1990, Crabtree 1988). There is also a suggestion that coyote territories have a longevity of their own that exceeds that of individual occupants.

Studies of relatively unexploited populations (Crabtree 1988, Gese et al. 1989) suggest 75-90% overall annual survival of adult coyotes in such situations may not be unusual. On age-specific basis, mean annual survival estimates from 3 field studies (Knowlton 1972, Crabtree 1988, Windberg 1995) indicate annual survival rates increase from about 0.40 in year 1 to about 0.70 by age 3, followed by a 2-3 year plateau and a decline thereafter, gradually at first and precipitously around age 10. Coyotes as old as 13, 14, and 15 years (Gese 1990, Knowlton unpubl. data) have been reported, but individuals over 11 are rare (Knowlton 1972, Gese 1995).

Recruitment into the adult portion of unexploited populations appears to be relatively low. One unexploited coyote population in eastern Washington had recruitment rates below 10%, with some coyotes apparently maintaining territoriality well into reproductive senescence (Crabtree 1988). Another study (Gese et al. 1989), reported low recruitment into a saturated, unexploited population as a result of low reproduction among yearlings, small litter sizes and high pup dispersal. Windberg et al. (In draft) provide data from a very lightly exploited population in southern New Mexico where juveniles composed only 7% of a population sample ($n = 44$) 1 year; a sample ($n = 38$) the next year failed to detect any juveniles. Although these data are meager, they suggest a pattern where reproductive rates among saturated populations fall far short of the biotic potential for the species.

The mechanics of change

While food abundance seems to set the ultimate limits of coyote abundance, and sociality is the driving force for change, proximate effects on density are linked to changes in reproduction, mortality, ingress and egress. A closer look at some of these components is warranted.

Reproductive performance. This component is associated with the fraction of the females breeding, mean litter size of reproductively-active females, and survival of offspring to some specific age. Data are sufficiently sparse and interactions sufficiently complex that unraveling details about factors influencing these parameters is impractical in this discussion. All 3 vary both among coyote populations and within populations over time. There is little doubt that prey abundance and population

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density are major influencing factors. Coyote populations seemingly have the potential to triple or quadruple density on an annual basis. On a practical level, however, exponential annual growth in excess of 0.6 appears unusual.

The generality seems to be that being dominant within a territorial social group is a prerequisite to reproductive success, with each territory trying to produce one litter each year. Hence the average size of social groups and the fraction of the population that belongs to territorial groups are important considerations. Some subordinate and non-territorial females may initiate the reproductive process, but most are doomed to fail.

Food abundance appears to be an important arbiter of litter size, especially in exploited populations. Placental scar count data from Curlew Valley, Utah, indicated that mean litter size varies from less than 4 to over 8 as a function of food abundance (Knowlton, unpubl. data). There was also a hint that mean litter size may be correlated with food conditions under which females are reared, as opposed to conditions leading up to specific reproductive seasons (Knowlton and Stoddart 1983).

Mean litter size, however, can hardly be the defining parameter, because the fraction of placental scars represented by juveniles in fall may vary by a factor of 5. Similarly, Crabtree (1988), Gese et al. (1989), Windberg (1995), and Gese (1995) identified juvenile survival as a major component of coyote demography. At the same time, coyote abundance apparently is a major factor regulating juvenile survival rates (Windberg 1995, Knowlton and Stoddart, unpubl. data). Better data related to reproductive performance and juvenile survival are needed.

Mortality. Mortality of adult coyotes, as determined by population age structures, tends to be higher among younger ages classes (1-2 years of age) and relatively older animals ($\geq$ 8 years of age). Conversely, survival appears to be high among coyote 3 to 7 years of age, especially among individuals that maintain associations with territorial groups. Causes of mortality among adult coyotes is closely linked with human activities (Knowlton and Stoddart 1983). This results both from direct exploitation (e.g. hunting, trapping, and related activities) and indirectly through collisions with automobiles, encounters with domestic dogs, etc. Recent studies (Windberg et al. 1985, Crabtree

1988, Gese et al. 1989, Windberg and Knowlton 1990) reinforced these interpretations.

Ingress and egress. Immigration and emigration are part of the dispersal process and occur when individuals enter or leave a population of interest. It is probably the least studied demographic aspect of coyote populations.

The relative frequency, as well as the distances moved, tend to be greater in more saturated populations than less saturated populations, resulting in net movements away from the former and toward the latter (Davison 1980). Hypotheses generated by Knight (1978) and Davison (1980) suggesting that low-ranking individuals are more likely to disperse have been validated by Gese (1995).

Dispersal is driven by nutritional and social interactions. Low-ranking individuals leave natal packs while high-ranking individuals are philopatric, biding their time for the dominant, breeding position. When food is abundant, more animals remain in the pack while in years of scarcity, more individuals disperse and pack sizes remain small. During periods of severe food scarcity, territorial behavior may be abandoned, with all members of social groups dispersing (Mills and Knowlton 1991, Grothe, unpubl. data).

Looking toward the future

There is a need to reassess our knowledge of coyote population biology and management through the revision of existing, or the creation of new, simulation models. Simulation models of animal populations help organize our understanding of the way populations function and provide a means for examining and exploring various concepts and ideas related to population management. It has been 20 years since Connolly and Longhurst (1975) and Connolly (1978) published and/or reviewed simulation models for coyote populations. These remain the simulation models currently available for coyote populations. They rely upon data collected in the late 1960s and published in the early 1970s, and utilize a series of equations linking demographic parameters, namely density, reproduction and mortality as understood at the time.

Relative coyote abundance was based upon fall rather than spring (stock) estimates and the impact of social constraints upon demographic parameters

were either unknown or excluded from the process. The data were obtained largely from populations subjected to human exploitation. These models were generated in the absence of information about the structural and functional aspects of populations not subjected to human exploitation. It is time to review the modeling process.

Several considerations should be incorporated into any new population modeling effort. Two important "data gaps" require study; namely (1) the effect of human exploitation (essentially increased mortality rates) on demographic and behavioral parameters; and (2) validation of characteristics of unexploited coyote populations. The latter is essential to provide a natural "endpoint" for a model, which figuratively represents the alternate extreme from the biotic potential of coyotes.

The possibility of using a behavioral, rather than demographic, base should be explored for a new coyote population model. Population models are usually developed to depict, or understand, changes in abundance or density. Incorporating behavioral constraints into a demographic model can be intimidating, especially since many behavioral aspects have not been defined mathematically.

However, population density could use 3 alternate parameters instead: mean territory size, mean number of individuals per territory, and percent of the population belonging to territorial groups. This would utilize the units by which coyote populations are structured and involve parameters that are more readily estimated than behavioral interactions with demographic variables. Some newer computer programming languages that involve "objects and attributes" may provide a useful programming medium for such endeavors in place of the equation-based programming techniques used previously. It will be interesting to watch the outcome of such endeavors.

An appropriate simulation model would be a useful tool in assessing merits of various management strategies as well as to help guide research efforts toward developing more effective and efficient depredation control techniques.

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